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Response to Leaf Inoculations with *Macrophomina phaseolina* in White Clover

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ABSTRACT

Summers in the southeastern USA produce a harsh environment for survival of white clover (*Trifolium repens* L.) stolons. Long periods of drought and hot temperatures are interspersed with rain showers that create ideal conditions for fungal pathogenesis. Previous studies indicated that *Macrophomina phaseolina* (Tassi) Goidanich may be an important pathogen that limits survival of white clover stolons in the summer. The objective of this study was to determine the range in response of 20 white clover cultivars, germplasms, and breeding and naturalized populations for resistance to *M. phaseolina* using a leaf tissue assay. Discs were cut from leaves excised from 50 plants of each entry and inoculated with an agar plug cut from the margin of a *M. phaseolina* colony. Leaf discs were scored according to the rate of necrosis induced by the pathogen. The experiment was conducted as a randomized complete block with four replicates and was repeated with 50 additional plants from each entry. Differences in responses of entries to inoculation with *M. phaseolina* were observed in each run of the experiment. Brown Loam Syn. 2 germplasm and North GA population had the least disease and the greatest number of plants selected as resistant to *M. phaseolina*. Large-leaf plants selected for resistance gave highly consistent responses when retested, with 35% of the plants having no leaf necrosis following inoculation with *M. phaseolina*. The leaf tissue assay was not as reliable for selecting consistent resistant phenotypes among small-leaf white clover entries, as 37% of the plants selected as resistant were rated as susceptible upon retesting. Resistance to *M. phaseolina* was observed in adapted white clover germplasm, and development of new cultivars with this resistance should improve white clover summer survival.

STOLONS are the means by which individual white clover genotypes persist in the field. The seedling taproot system only survives for the first year or two of growth. When the taproot, primary stem, and basal portion of the stolons die, plant survival is entirely dependent on new stolon growth from the terminal ends. Individual stolons from the same plant are genetically identical, but may no longer be connected. New growth and branching continues at the stolon tips while the older basal portion of the stolon dies. The genotype will survive as long as new stolon growth at the tip exceeds the progression of necrosis from the basal end.

White clover plants face a number of biotic stresses, including viruses, insects, fungi, and nematodes, that reduce stolon and plant vigor (James et al., 1980; Pederson, 1995; Pederson et al., 1991). In the southeastern

USA, environmental stresses include saturated soils in the winter and hot, drought conditions in the summer. Though environmental and other factors can reduce white clover growth and stands at any time of the year, complete death of the stand usually occurs in the summer (Gibson and Hollowell, 1966).

Fungal disease pressure plays an integral role in the survival of white clover stolons in the summer. The normal summer environment of the southeastern USA is ideal for fungal pathogenesis. Fungicides have been shown to improve white clover yield and persistence (James et al., 1980; Pederson et al., 1991). Fungicide treatment during the summer months improves white clover stolon density, growing point density, and stolon length (Pederson and Pratt, 1995). Germplasm sources differ in their response to fungicide treatment; Brown Loam Syn. 2 germplasm showed less response to fungicide treatment than 'Regal' and 'Louisiana S-1' white clover (Pederson and Pratt, 1995). These data suggest that this germplasm may have some resistance or tolerance to summer fungal diseases. Naturalized populations that have survived in pastures for a number of years have also been suggested as sources of resistance or tolerance to summer stolon diseases (Cope, 1978).

Numerous fungi are frequently isolated from white clover stolons including *Colletotrichum* spp., *Curvularia trifolii* (Kauff.) Boedijn, *Fusarium* spp., *Mycoleptodiscus terrestris* (Gerdemann) Ostazeski, *M. phaseolina*, *Rhizoctonia* spp., *Sclerotium rolfsii* Sacc., and others (Halpin et al., 1963; Latch and Skipp, 1987; McGlohon, 1959; Pederson and Pratt, 1995). The relative importance of individual fungal species for stolon survival has rarely been addressed. Some fungi appear to play no active role in stolon necrosis, arriving only as secondary pathogens when death and decay have already begun. Other fungi may be quite pathogenic. Following a previous study of white clover stolon growth with and without fungicide treatment (Pederson and Pratt, 1995), Pratt (1998, unpublished data) evaluated the pathogenicity of 200 fungal isolates to identify highly pathogenic fungal species and isolates. Two of the most pathogenic isolates were identified as *M. phaseolina*. This fungus was pathogenic to mature white clover tissue including both stolons and excised leaves (Pratt et al., 1998). In stolons, radically constricted brown-black lesions developed and progressed longitudinally. In excised leaf tissue, necrosis spread evenly across the leaf disc, starting at the basal end where inoculation occurred. The necrotic tissue had a collapsed water-soaked, light green appearance as opposed to the dark green healthy tissue (Pratt et al., 1998). Differences in rate of parasitism were observed

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Table 1. White clover entries evaluated for resistance to *Macrophomina phaseolina*.

Entries	Plant type	State of origin	Characteristics (reference) [†]
Cultivars			
Louisiana S-1	Intermediate	LA	Selected for heat and drought tolerance (b,c)
Osceola	Large	FL	Selected for flower production and summer persistence (b,c)
Regal	Large	AL	Selected for summer production and persistence (b,c)
Germplasms			
Brown Loam Syn. 2	Large	MS	Selected for drought tolerance and summer survival (c)
MSNR4	Intermediate	MS	Root-knot nematode resistant (c)
SRVR	Large	SC, NC, VA	Multiple virus resistant (c)
Breeding populations			
CercoF ₂	Large	NC	F ₂ population of <i>Cercospora</i> resistant × susceptible plants (e)
LF-1	Large	MS	Selected for flower production (e)
NC-7	Large	NC	High forage production population (e)
VRG	Large	MS	Selection for field persistence from SRVR (e)
VR18 × 36	Large	MS	Multiple virus resistant population (e)
WC1	Large	MS	Selection for field persistence from plant introductions (e)
Naturalized (pasture collected) populations			
Alabama	Small	AL	Collected from ten Alabama pastures (a,d)
North GA	Small	GA	Collected from two pastures in Eatonton, GA (a,d)
South GA	Small	GA	Collected from a pasture in Tifton, GA (a,d)
Homer 1 LA	Small	LA	Collected from a pasture in Homer, LA (f)
Homer 2 LA	Small	LA	Collected from volunteer plants at Homer, LA (f)
Starkville MS	Small	MS	Collected from five pastures near Starkville, MS (a,d)
Pontotoc MS	Small	MS	Collected from four pastures near Pontotoc, MS (a,d)
Raymond MS	Small	MS	Collected from three pastures near Raymond, MS (a,d)

[†] Letter in parentheses is the reference source of characteristic information: a = Brink et al., 1999; b = Caradus, 1986; c = Caradus and Woodfield, 1997; d = Pederson and Brink, 1997; e = Pederson, 1998, unpublished data; and f = B.C. Venuto, 1994, personal communication.

between genotypes. These observations suggested that rates of parasitism by *M. phaseolina* in excised leaf tissues might be used to evaluate and select for resistant responses in white clover populations.

The objective of this study was to determine the range in response of 20 white clover cultivars, germplasms, breeding populations, and naturalized populations for resistance to *M. phaseolina* by using a leaf tissue assay. Breeding and naturalized populations included in this study had been selected for field persistence and thereby possible fungal disease resistance.

MATERIALS AND METHODS

Twenty cultivars, germplasms, breeding populations, and naturalized populations were used in this study (Table 1). Ten white clover entries were large-leaf type and ten were small to intermediate type. Seed of naturalized populations was produced from cage-seed increases of populations collected in closely grazed pastures in Alabama, Georgia, Louisiana, and Mississippi.

Initial Resistance Evaluation

Fifty plants of each entry were grown in the greenhouse at Mississippi State, MS. All leaves were cut from each plant 8 d prior to inoculation. The second fully expanded leaf from a growing stolon tip was harvested and a 13-mm-diameter disc was cut from the terminal leaflet with a cork borer. The disc was placed on a 35-mm-diameter petri plate containing water agar. Each leaf disc was inoculated with a 6-mm-diameter agar plug cut from the margin of a *M. phaseolina* colony growing on corn meal agar. The agar plug was inverted onto the base of the midvein of the leaf disc such that the mycelia were growing toward the cut edge of the leaf. The plates were placed on a lab bench at 24°C for 7 d. Leaf discs were scored on a 0 to 7 scale for rate of necrosis caused by *M. phaseolina*, with 7 = completely necrotic on Day 1, 6 = necrotic on Day 2, 5 = necrotic on Day 3, 4 = necrotic on Day 4, 3 = necrotic on Day 5, 2 = necrotic on Day 6, and 1 = necrotic on Day 7. Leaves not completely necrotic by the seventh day were

scored from 0.1 to 0.9 according to the proportion of the leaf disc that was necrotic. Leaf discs with no necrosis by the seventh day were scored 0 (Pratt et al., 1998).

One leaf from each plant was inoculated in Run 1 on 28 May, 27 June, 15 August, and 18 Sept. 1996. Each date was considered a replicate. The experiment was repeated (Run 2) with 50 different plants of each entry. Run 2 inoculations were conducted 25 October, 15 November, and 13 Dec. 1996, and 24 Jan. 1997.

The experimental design was a randomized complete block with four replicates. Due to significant run × entry interactions, the data were analyzed separately for each run of the initial resistance evaluation (SAS Institute, 1990). Means were compared by Fisher's protected least significant difference. Unless otherwise noted, the 0.05 level of probability was used to determine differences.

Retesting of Putative Resistant Plants

Selections for additional testing were made of the most resistant 100 large-leaf and 100 small-leaf plants from each run of the initial resistance evaluation. Large-leaf plants selected as resistant in the initial test had a mean disease score ≤0.95 in Run 1 or ≤1.05 in Run 2 and no disease score >2 in any replicate. Small-leaf plants selected as resistant in the initial test had a mean disease score ≤1.22 in Run 1 or ≤0.95 in Run 2 and no disease score >2 in any replicate. Some plants died prior to retesting, so a total of 188 large-leaf plants (95 from Run 1 and 93 from Run 2) and 174 small-leaf plants (82 from Run 1 and 92 from Run 2) were retested for resistance. This experiment was conducted as in the initial resistance evaluation except that five leaf discs (replicates) were cut from terminal leaflets of second fully expanded leaves from stolon tips of each plant and placed on water agar in 100-mm-diameter petri plates. Large-leaf plants were inoculated on 14 Feb. 1997 and small-leaf plants were inoculated on 7 Mar. 1997. One susceptible plant from each entry in Runs 1 and 2 was also inoculated (20 small-leaf and 20 large-leaf plants) in the retesting. Leaf discs were scored in the same manner as in the initial resistance evaluation. Plants in the retesting experiment with mean disease scores ≥1.5 or a disease score >2 in any

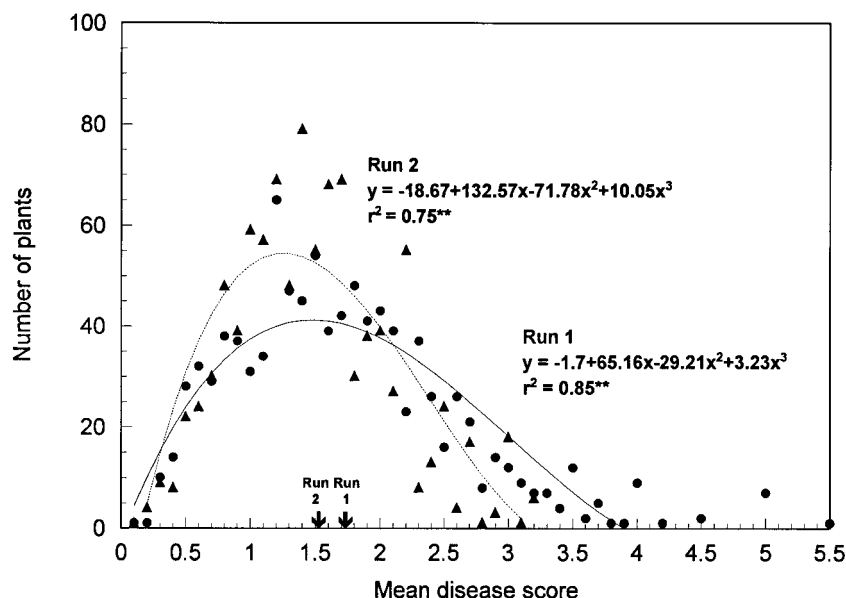


Fig. 1. Mean disease scores (0–7, 0 = no necrosis) of excised leaf discs from Run 1 (circles) and Run 2 (triangles) of 50 plants each from 20 white clover cultivars, germplasms, and populations inoculated with *Macrophomina phaseolina* in initial resistance evaluation. Arrows indicate the mean disease score for each run.

replicate were assumed to be escapes from the initial resistance evaluation and were considered susceptible.

Regression analysis was conducted to compare distribution of disease scores within runs in the initial resistance evaluation and to compare distribution of disease scores of large- and small-leaf selections in the retesting experiment. Coefficients were included in a regression equation when the coefficient was significant at the 0.05 level and the increase in equation order increased the R^2 by at least 5%.

RESULTS

Initial Resistance Evaluation

Differences were observed between the two runs and a run \times entry interaction was found for mean disease score following inoculation with *M. phaseolina*. The mean disease score was greater in Run 1 (1.72 ± 0.02 ; mean \pm SE) than Run 2 (1.53 ± 0.02). The mean disease scores for individual plants in Run 1 ranged from 0.1 to 5.5, while in Run 2 the range was only 0.1 to 3.2 (Fig. 1).

In Run 1, Brown Loam Syn. 2 had the lowest disease score, which was lower than all entries except CercoF₂, NC-7, and WC1 (Table 2). Homer 1 LA had a greater disease score than all entries except MSNR4. Differences were also observed among the four inoculation dates in Run 1, with the highest disease scores observed from the 15 August inoculation and the least from the 27 June inoculation (data not shown).

North GA had the lowest disease score in Run 2, which was lower than all entries except Pontotoc MS (Table 2). Regal had a greater disease score than all other entries in this run. The highest disease scores in Run 2 were observed from the 25 October inoculation and the least from the 13 Dec. 1996 and 24 Jan. 1997 inoculations (data not shown).

The run \times entry interaction was most noticeable for North GA, VR18x36, and Pontotoc MS populations,

which all ranked rather high for disease score in Run 1 and low for disease score in Run 2 (Table 2). Some entries were consistent between runs: Brown Loam Syn. 2 consistently had a low disease score (1.21 ± 0.09 and 1.26 ± 0.07), and MSNR4 (2.28 ± 0.10 and 1.89 ± 0.08) and Regal (1.95 ± 0.12 and 2.14 ± 0.09) consistently had relatively high disease scores.

The 100 most resistant large-leaf and small-leaf plants from each run of the initial resistance evaluation were selected for additional testing (Table 3). Selection was based on lowest mean disease score and no disease score >2 in any replicate. Brown Loam Syn. 2 had the greatest number of resistant plants of the large-leaf types and North GA had the greatest number of the small-leaf types. As susceptible checks, the most susceptible plant from each entry in Run 1 and 2 was selected.

Retesting of Putative Resistant Plants

Selected plants were retested to eliminate susceptible plants that failed to develop severe disease symptoms in the initial resistance evaluation. Large-leaf white clover entries had few escapes, as only 7% of the putative resistant plants from the initial test were rated as susceptible during retesting (Table 3). Most of the selected large-leaf plants were highly resistant in the retesting experiment, with 35% of the plants having no necrotic leaf tissue (mean disease score = 0; Fig. 2). Of the small-leaf entries, almost 37% of the plants selected as resistant in the initial test were determined to be susceptible during retesting. Only one small-leaf plant had no necrotic leaf tissue and the selected plants showed a wide distribution of mean disease scores (Fig. 2). The mean disease score of 0.35 ± 0.02 for the 188 large-leaf plants was lower than the 1.25 ± 0.04 mean disease score for the 174 small-leaf plants. Both small- and large-leaf resistant selections had lower disease

Table 2. Leaf necrosis scores for white clover cultivars, germplasms, breeding populations, and naturalized populations in response to *Macrophomina phaseolina* in Runs 1 and 2 of the initial resistance evaluation.

Entries	Run 1		Run 2	
	Mean†	Range of mean scores	Mean†	Range of mean scores
Large-leaf				
‘Osceola’	1.72	0.45–3.42	1.68	0.35–3.00
‘Regal’	1.95	0.35–5.00	2.14	1.02–3.25
Brown Loam Syn. 2	1.21	0.20–3.30	1.26	0.28–3.00
SRVR	1.58	0.35–3.12	1.59	0.55–3.25
CercoF ₂	1.32	0.37–2.80	1.48	0.40–2.75
LF-1	1.84	0.50–4.00	1.52	0.55–2.45
NC-7	1.41	0.45–3.40	1.56	0.55–3.00
VRG	1.61	0.18–3.92	1.67	0.62–3.12
VR18 × 36	2.05	0.52–4.00	1.43	0.35–3.33
WC1	1.46	0.40–3.18	1.47	0.62–3.00
Small-leaf				
‘Louisiana S-1’	1.69	0.48–3.75	1.83	0.90–3.25
MSNR4	2.28	0.80–4.25	1.89	0.52–3.33
Alabama	1.57	0.60–5.50	1.48	0.25–2.50
North GA	1.87	0.58–3.72	0.98	0.30–2.25
South GA	1.53	0.65–3.75	1.41	0.58–2.25
Homer 1 LA	2.35	0.75–5.00	1.57	0.80–3.00
Homer 2 LA	1.56	0.33–5.00	1.60	0.55–3.00
Starkville MS	1.98	0.43–5.00	1.52	0.28–3.25
Pontotoc MS	1.77	0.68–3.35	1.12	0.12–2.20
Raymond MS	1.78	0.78–3.50	1.33	0.30–2.50
LSD 0.05	0.25		0.20	

† Mean score for rate of leaf necrosis by *M. phaseolina* with 7 = complete necrosis on the 1st day, 6 = necrotic on 2nd day, 5 = necrotic on 3rd day, 4 = necrotic on 4th day, 3 = necrotic on 5th day, 2 = necrotic on 6th day, and 1 = necrotic on 7th day. Leaves not completely necrotic by the 7th day were scored from 0.1 to 0.9 for percentage of the leaf disc that was necrotic. Leaf discs with no necrosis by the 7th day were scored 0.

Table 3. Number of resistant plants selected in the initial resistance evaluation and number of escapes found during retesting of putative resistant plants from 20 white clover cultivars, germplasms, breeding populations, and naturalized populations evaluated for resistance to *Macrophomina phaseolina*.

	Number of resistant plants selected in initial evaluation†	Number of escapes found during retesting‡
Large-leaf		
‘Osceola’	18	0
‘Regal’	6	0
Brown Loam Syn. 2	40	1
SRVR	14	0
CercoF ₂	24	3
LF-1	14	1
NC-7	19	1
VRG	16	2
VR18 × 36	17	1
WC1	20	4
Total	188	13
Small-leaf		
‘Louisiana S-1’	11	5
MSNR4	4	2
Alabama	21	8
North GA	32	11
South GA	26	6
Homer 1 LA	6	2
Homer 2 LA	19	8
Starkville MS	17	3
Pontotoc MS	18	11
Raymond MS	20	8
Total	174	64

† Large-leaf plants were selected as resistant in initial resistance evaluation with a mean disease score ≤0.95 in Run 1 or ≤1.05 in Run 2 and no disease score >2 in any replicate. Small-leaf plants were selected as resistant in initial resistance evaluation with a mean disease score ≤1.22 in Run 1 or ≤0.95 in Run 2 and no disease score >2 in any replicate.

‡ Plants in the retesting of putative resistant plants with mean disease scores ≥1.5 or a disease score >2 in any replicate were assumed to be escapes from the initial resistance evaluation and were considered susceptible.

scores than those of the susceptible small- (1.86 ± 0.22) and large-leaf (1.91 ± 0.19) controls.

DISCUSSION

White clover stolons in the hot humid summers of the southeastern USA are often in a race for survival against fungal necrosis. The terminal stolon tip needs to grow as rapidly as possible during favorable conditions to stay ahead of necrosis spreading up the basal portion of the stolon. If necrosis reaches the tip before the end of summer, the race is over and that portion of the plant dies. If necrosis reaches the tips of all stolons, the white clover stand is eliminated.

Selection for resistance to individual stolon fungal pathogens would seem to be an obvious way to reduce the effect of fungal necrosis on white clover stolon survival. However, selection for resistance has rarely been attempted due to the numerous fungal species that can be isolated from white clover stolons. Determining which of these fungal pathogens are important components in the stolon-rotting disease complex is difficult. Too often “importance” has been based on which fungal species were isolated most often. Garren (1955) reported that more than 50% of isolates obtained from damaged stolons in the summer were *Fusarium* and *Rhizoctonia* spp. McGlohon (1959) found that 70% of isolates collected from white clover stolons in the summer were *Fusarium*, 17% were *Rhizoctonia*, and 4% were *Macrophomina* spp.

Pathogenicity studies of a few fungal species have been conducted on white clover, though these evaluations often relied mainly on white clover vigor and persistence. McCarter and Halpin (1962) concluded that *S.*

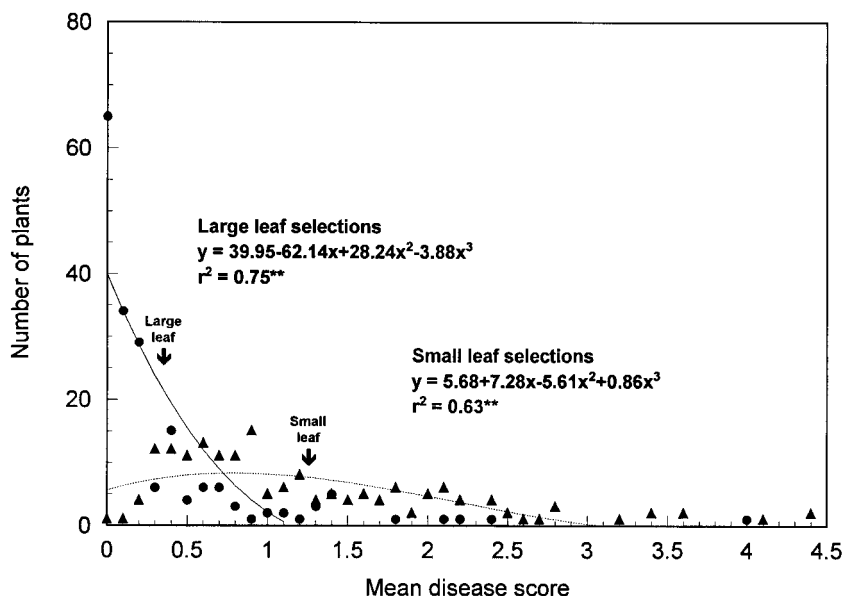


Fig. 2. Mean disease scores (0–7, 0 = no necrosis) of excised leaf discs from large-leaf (circles) and small-leaf (triangles) white clover plants selected for resistance to *Macrophomina phaseolina* in the initial resistance evaluation and inoculated with *M. phaseolina* for retesting of putative resistant plants. Arrows indicate the mean disease score of large- and small-leaf plants.

rofsii was more pathogenic at high temperatures (23 and 30°C) than eight other fungal species and Halpin (1963) reported that *S. rofsii* was more pathogenic on white clover than five other fungal species. However, Halpin et al. (1963) reported that damage by *S. rofsii* was often secondary in nature, occurring subsequent to summer stolon death caused by numerous soil fungi. None of these tests evaluated *M. phaseolina* for pathogenicity. Some fungi probably do not play an active role in stolon necrosis, arriving only as secondary pathogens when death and decay have already begun. Rapidity of mature tissue decay is the key factor in addressing the relative importance of fungi as pathogens of white clover stolons. Our previous work demonstrating the pathogenicity of this species on mature white clover tissue (Pratt, 1998, unpublished data; Pratt et al., 1998) has clearly established *M. phaseolina* as one of the important fungal pathogens of white clover stolons.

Performance of the germplasms in this study relate quite well to visual observations of plant survival during the summer in Mississippi field studies. Brown Loam Syn. 2 has consistently been the best performing white clover following the summer drought in the field in Mississippi (Pederson and Pratt, 1995), while MSNR4 dies out more rapidly than other white clovers during the summer drought (Pederson and Windham, 1995, unpublished data). In this study, Brown Loam Syn. 2 consistently had a low disease score following inoculation with *M. phaseolina*, and 33 resistant plants were selected from it for further crossing. MSNR4 consistently had a high disease score, and no resistant plants were selected for further crossing. Though we would not suggest that resistance to *M. phaseolina* is the only reason these germplasms survive or do not survive the summer, these results certainly suggest that resistance or susceptibility to this pathogen plays a role in their survival. Field testing of the populations developed from

this study will provide more information on the importance of this pathogen in white clover stolon survival in the summer.

The naturalized populations did not have any greater level of resistance to *M. phaseolina* than the other entries tested (Table 2). North GA was the most resistant of the populations in Run 2, but was more susceptible than three of the other populations in Run 1. All eight of the naturalized populations flower profusely and produce large amounts of seed (Pederson and Brink, 1997). It is possible that seedling recruitment may be a major mechanism of stand persistence of these populations rather than summer stolon survival by virtue of fungal disease resistance.

There was a great difference between the large- and small-leaf plants in the reliability of evaluating resistance by the leaf-tissue test (Table 3). Leaves selected from small-leaf plants sometimes were <13 mm in diameter; therefore, less leaf tissue was available for parasitism. The tissue used may not have been as succulent as that obtained from the large-leaf plants due to slower recovery of the small-leaf plants from defoliation. Accurate placement of the agar plug containing *M. phaseolina* mycelium was more difficult on the small-leaf discs. These factors resulted in a larger number of escapes (37%) in the small-leaf plants than in the large-leaf plants (7%). Methods will need to be refined to more adequately evaluate response to *M. phaseolina* in small-leaf white clover. Conditions in the greenhouse during the 8 d prior to inoculation also affected the results from the leaf tissue test. Leaves sampled from plants during a period of active growth had higher disease scores than leaves sampled from plants during a relatively inactive period of growth. This resulted in replicate and run differences when the tests were conducted at different times during the year.

Relationships of resistance to *M. phaseolina* in excised

leaf tissues and in intact stolons, where meaningful pathogenesis occurs in the field, have not yet been fully determined. However, in preliminary experiments (Pratt, 1998, unpublished data), progeny of plants selected for *M. phaseolina* resistance in excised leaf tissues exhibited both greater resistance in leaf assays and also less systemic invasion of stolons than unselected plants following uniform stolon inoculations in the greenhouse. These observations suggest that reduced rates of parasitism observed in excised leaf tissues are associated with reduced systemic invasion of stolons in plants. Further efforts to define these relationships are in progress.

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